

## CIVIL DISTURBANCES IN ANT COMMUNITIES

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It is not so long ago that the title of this paper would have seemed almost paradoxical, as ants were believed to be perfectly social. Recently, however, new observations and the collection of previously recorded incidents have not only made it clear that civil disturbances do occur, but have also indicated that there may be a variety of motivation for them. It is the purpose of this paper, not merely to add to the recorded list of civil disturbances, but also to detail the probable motivations thereof.

First, a word or two may be devoted to the question of recognition. We are concerned with the deliberate attack by one ant upon a nest-mate, but the appearance of such an attack could readily be produced by one ant's failure to recognize a nest-mate as such, and her consequent attack upon her as an enemy. If a strong perfume is sprinkled over ants it interferes with their power of recognition: in most cases it causes the ant, depending upon its species and individual attitude, to treat strangers as friends, or, *per contra*, to treat its friends as enemies. A similar result is sometimes produced by poisons, such as corrosive sublimate, and by the amputation of the antennæ. Brain lesions or disease might well have the same effect. When individual ants are handled, or sprayed with poison by hostile ants, or when they fall into honey or even into water, it sometimes causes their comrades to fail to recognize them, and temporary "arrests" or more serious attacks may then occur. In a very large nest, recognition, if based on individual characteristics, as must be the case in at least some cases (*e.g.*, those where individuals of other species have been adopted), might fail at times due to the number of individuals involved. It therefore becomes necessary to take every precaution lest a case of mistaken identity be listed among the instances of deliberate attack on a nest-mate, I have taken such precautions, and none of the incidents referred to in this or in previous articles on the same topic may reasonably be ascribed to a failure in recognition.

Certain cases of civil disturbance have the appearance of being the deliberate punishment by some ants of nest-mates who fail to defend the nest. The psychological implications of such behavior are so startling that one naturally hesitates to accept them, but the behavior itself is well attested and no alternative explanation has as yet been offered. This problem is discussed in "Punitive Behavior of Ants."<sup>1</sup>

Sometimes the conduct of individual ants has all the characteristics that attend human cruelty or even sadism. Some instances of this type of conduct are discussed in an article entitled "Anti-Social Behavior of Ants."<sup>2</sup> Since the writing of that article, a further incident has occurred in my nests which may be of this type, and which merits recording. I had a nest containing a queen and three workers of *Formica subsericea* to which, from time to time, I introduced some young of *Formica neocinerea*. The first of these alien ants was born into the nest on March 16, the second on March 17, and a third on April 10. These workers behaved and were treated precisely as would ants that were progeny of the queen. On the evening of April 15 the fourth *neocinerea* was born, the *subsericea* queen died on the night of April 17-18, and on April 18 one of the older *neocinerea* was observed attacking her callow sister. The attack was persistent, until I separated them by force after a few hours. The attack was not then repeated. This affair was exceptional, since the participants were not only nest-mates and blood-sisters, but also because they were so very young. A newly born worker is hardly ever attacked by any ant of its own or a closely allied species, regardless of the nest of origin.

I have observed that fighting frequently breaks out between affiliated queens in an incipient nest, and the timing of these outbreaks strongly suggested to me that the motivation was jealousy between the queens for the loyalty of the brood. This was discussed in "Communal Disaffection in Ants."<sup>3</sup> Since the publication of that article I have found that a similar case was re-

<sup>1</sup> Journal of Comparative Psychology, Vol. 29, No. 3, p. 327, June 1940.

<sup>2</sup> To be published in The Journal of Comparative Psychology.

<sup>3</sup> Journal of the N. Y. Entomological Society, Vol. XLIX, p. 199, June 1941.

ported by von Buttler-Reepen, where two *Lasius niger* queens fought shortly after the birth of their first young, although they had lived peacefully together for almost a year.<sup>4</sup>

There are times when it may seem to be to the communal interest to dispose of certain members of the community, as is the case with drones among the bees. Indeed, it has been reported that some ants similarly dispose of any males that may be left after the annual swarming. Sterile queens are almost as useless, and Brun, who observed the workers in a nest of *Lasius niger* kill one of two adopted queens, believes this conduct to be the result of the victim's sterility.<sup>5</sup> While Brun's conclusions may well be correct, his data are hardly sufficient to validate his hypothesis. It is supported, nevertheless, by some associated facts. In some cases of formicine parasitism, the workers regularly kill off their own queens in favor of the parasitic queens; presumably because the latter are smaller and require less sustenance. Forel suggests that *Formica fusca* slaves may object to the food consumption of their *Polyergus* masters in times of scarcity, and relates a fatal disturbance that resulted from this.<sup>6</sup>

Another case, though incompletely authenticated, occurred in the Bronx zoo this past winter. For some time a nest of the leaf-cutting *Atta* has been housed in the reptile house, where the lines of leaf-bearing ants is a great public attraction. To increase the showiness of the spectacle, the zoo provided roses of different colors, in the expectation that the various colors of petals and the green leaves would provide a brilliant show. Unfortunately the ants decided otherwise, and confined themselves to the yellow petals, taking the red ones only after the yellow were exhausted, and the leaves only when everything else was gone. This year it was decided that the ants should be given fallen petals as an economy measure, whereupon the ants went on a hunger strike. It was the habit of this colony to deposit its dead during the night, and the death rate increased during this period to several hundred a day. It was suggested that the ants

<sup>4</sup> Archiv für Rassen- und Gesellschafts- Biologie, 1905, pp. 24-31.

<sup>5</sup> Biologisches Centralblatt, 1912, p. 163-167.

<sup>6</sup> International Monthly, Vol. 5, p. 721-722, Burlington Vt., 1902. Republished in "Punitive Behavior of Ants," *q. v.*

deliberately reduced their number in view of their depleted food resources, but unfortunately there is no direct evidence on this point, however probable it may seem. The arrangements in the reptile house are such that no glimpse of the interior of the nest is possible, and even the exterior was not observed during the night. As soon as living roses were again supplied, the death rate was reduced to the normal. Reports of these events that appeared in the newspapers inferred that the workers were eating each other in lieu of other food, and although this is highly improbable, there is no direct evidence to refute it. It is much more likely that the corpses would be used as fertilizer for the fungus beds as it is known that these ants use their own excrement for this purpose. But even this is hardly to be accepted as there was no indication, on the discarded corpses of the ants, of actual violence. Perhaps this is putting it too strongly: the correct statement is only that the officials at the zoo do not remember any evidences of mutilation.

The suggestion of cannibalism, although unfounded in the case just considered must not be ignored when considering possible motivations for anti-social conduct. If ants may kill one another for other reasons including the reason that there is not enough food to go around, it would seem likely that they might do the same for cannibalistic use. Especially is this the case among ants that regularly feed on their own dead, as do *Formica subsericea*. There is, however, no evidence of such behavior, though it is a well-nigh universal practice of ants to use their larval forms as food when necessary. Queens frequently eat their eggs in the early stages of the nest, and I have many times observed pupae similarly consumed. We might add that cannibalism is quite ordinary among the termites.

Janet has suggested that ants may kill one another for lack of space when they become overcrowded. This factor may well have been present in the case of the *Atta* already reported, and Janet himself describes *Solenopsis fugax* and *Tetramorium caespitum* as killing off supernumerary queens when expansion of the nest became impossible.<sup>7</sup> But even in a natural nest a

<sup>7</sup> Reported by Forel, in "The Social World of the Ants," Vol. 1, p. 428, Boni, N. Y., 1929.

similar thing may occur, for Bruch observed *Acromyrmex Lundi* kill fertile queens shortly after swarming time by cutting off their abdomens,<sup>8</sup> and Brauns observed fertile queens of *Messor meridionalis* driven out of their nests by workers or other queens.<sup>9</sup> It seems likely that all these instances are somehow related, and two hypotheses come to mind. Perhaps queens fertilized in the nest or returning to it after a nuptial flight are subsequently driven out with or without workers as a sort of colony-budding process. Of perhaps the new queens are accepted and the old ones, whose seminal vesicles may be exhausted or nearing exhaustion, are driven out or killed. On the other hand, Janet's hypotheses may be near the truth, and the ants may restrict their numbers to a limit determined by the species or by the resources of the vicinity.

If fighting within the community once starts, it might spread by imitation. In "Communal Disaffection in Ants" I have described how workers twice joined with one of their queens in an attack upon another. Jealousy, which is the presumed motive of the queens, would not apply to the workers, who may therefore have been following the cue given by the queen. This motive would also act to cause the observed continuity of disturbance noticed in the cases described in "Anti-Social Behavior among Ants" and in the present article and is, obviously, closely parallel to mob psychology among human beings.

There are, in addition to the ones we have already mentioned, cases of civil disturbances that do not fall into any of these six categories. By this I do not mean merely that it is uncertain in which category they belong; as would be true in the case where fertile queens were simultaneously expelled from many nests of the same species in a given locality; but that it is apparent that no one of the motivations previously discussed will explain the situation. An example involving this difficulty occurred among my nests recently. A fairly large nest of *Myrmica scabrinodis* was dug up by Mr. Windsor in Chicago on April 13, and received by me on April 19. On April 22 the ants were allowed to migrate from a temporary into a permanent nest, and on April 23 fourteen decapitated corpses were observed. Their deaths must all

<sup>8</sup> Revista del Museo de la Plata, 1921, p. 175-211.

<sup>9</sup> Forel, "The Social World of the Ants," Vol.2, p. 232.

have occurred within twenty-four hours. At the same time one worker was observed grasping another's neck, a grip which she maintained half an hour. At the end of that period the aggressor released her hold, and I noticed that both were treated normally by the other workers. After about a minute they met again, and the aggressor seized her victim's antenna, then her head, and then released her once more. After seven or eight minutes during which the two did not meet, I lost track of them in the crowd.

No further corpses were found the next day, nor were any subsequent attacks observed until May 9, when two workers were seen attacking a third. Some further fighting was observed around May 13, and again on May 28. These dates are not the only ones on which fighting occurred, since minor fighting was not always recorded and because the nest was observed rather infrequently.

On June 7 the fighting increased in intensity. Two pairs were observed, one in each pair chewing at the other's pedicel. After an hour and a half I used a glass to focus the sun's rays on the aggressors and they let go. At this time and subsequently, it was noticeable that when separated in this or in any other way the aggressor made no effort to find her victim, and when they met accidentally after separation no further fighting developed. In this and in almost every other way this case differs from the apparently deliberate cruelty of *Formica neocinerea*.

A few minutes after separating the two pairs mentioned above, another pair was observed in a similar struggle, but the victim wandered off when the aggressor let go to clean herself. Later two more pairs were observed, both grips being antennal, and after an hour and a half I separated them by the same method used before. On June 9 the nest was unobserved, but on the tenth there were several fighting pairs one of which could not be separated by the use of the glass, the aggressor being sufficiently tenacious to suffer sooner than to release her victim.

At this point it was evident that none of the categories discussed in this article would apply to this case unless it could be lack of space that induced the trouble, there being approximately four hundred ants in a nest of forty square inches. To test this hypothesis I connected the nest with an empty one of similar

construction and equal size expecting that, if the hypothesis were correct, the ants would either divide into two nests or use the new one as an antechamber. In either case the fighting should stop. But in fact the ants showed no great interest in the new nest, beyond the number of exploratory visits that would be expected in such a confined space. I then proceeded to divide the nest by force, putting two of the seven queens, a few young, and almost half the workers in the new nest. Although this involved handling many of the ants, no fighting was caused thereby, which helps to dispose of the possibility that the fighting might be caused by a failure of recognition. Finally the disturbances not only failed to disappear, but even increased somewhat in frequency and intensity in the succeeding days, several deaths occurring which were probably due to this condition. This was true, moreover, not only of the old nest where the pressure of population was much decreased but also in the new nest, where the actual population was less than half the original density, and the potential population distinctly inferior. The condition of casual fighting that was typical of the original nest thus continued to be true of both its successors. The hypothesis of spacial restriction is therefore untenable in this instance, and no other hypothesis is at present available to account for the facts.<sup>10</sup>

We have, then, four motives fairly well established as possible causes of civil strife among formicine communities: these are, punishment or pseudo-punishment, cruelty, jealousy, and the communal interest in disposing of such unneeded individuals as males or infertile or overlarge females. In addition there are other possible motives in lack of food, cannibalism, spacial limitation, and imitation. Even with this additional list of possible motives, however, it is clear that there is a residue of anti-social behavior that still awaits explanation.

<sup>10</sup> It is nevertheless possible, if highly improbable, that spacial restriction may have been responsible for originating the fighting which continued subsequently as a result of imitation.